

## Three new species of bathyal cidaroids (Echinodermata: Echinoidea) from the Antarctic region

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*Abstract.*—Two new species of *Aporocidaris*, *A. eltaniana* and *A. usarpi*, and one new species of *Notocidaris*, *N. lanceolata*, are described from material collected during United States Antarctic Research Program expeditions in the 1960's. All three species occur in the bathyal zone near or south of the Subantarctic Convergence. Gonopore sizes and peristomial morphology suggest that these species are sexually dimorphic and that the females can brood direct-developing young. However, only one of the *Aporocidaris* species was found to harbor embryos on the peristomial membrane.

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In the mid- to late 1960's, Dr. Richard H. Chesher, at the Museum of Comparative Zoology at Harvard (MCZ), studied echinoid material collected under the auspices of the United States Antarctic Research Program (USARP). The USARP, which began in 1955, included trawling and dredging expeditions by ships in the vicinity of Antarctica (Fig. 1). Material collected by the U.S. National Science Foundation Research Vessel R/V *Eltanin* is of particular importance to this paper. Dr. Chesher identified numerous USARP echinoids, in the process discovering several new species. In some cases, he proposed manuscript names and indicated type specimens for new species (for example, see David & Mooi 1990), but he was unable to continue systematic work after 1967, thereby leaving these names and manuscripts unpublished. Chesher's cidaroid research was incorporated into a dissertation (Fell 1976), and two of the species described below were covered in this work. As a result, several putative types for which no names have been published are deposited in the National Museum of Natural History (NMNH)—the major repository of echinoid collecting during

the USARP, and in the MCZ. Here, we publish these names for the first time.

Antarctic cidaroids are represented by approximately 20 species in 5 genera, and all belong to the subfamily Ctenocidarinae. With one or two exceptions, the ctenocidarines are restricted to the Antarctic and Subantarctic regions and are among the most diverse of the Antarctic echinoids. Although their taxonomy was hugely advanced in Fell (1976), an exact count of valid taxa is difficult, given the uncertain specific and subspecific status applied to the variants. We are currently engaged in a databasing project that will result in a comprehensive overview of all Antarctic echinoids, including cidaroids, and it was this review that prompted the work on the taxa described herein.

Much of the Antarctic cidaroid fauna still requires revision in a modern context. For example, the only recent attempt (Smith & Wright 1988) to resolve phylogenetic relationships among any of the cidaroids concentrated on Cretaceous forms, and did not deal with Antarctic taxa. Phylogenetic relationships among the different genera and species are still speculative and will remain

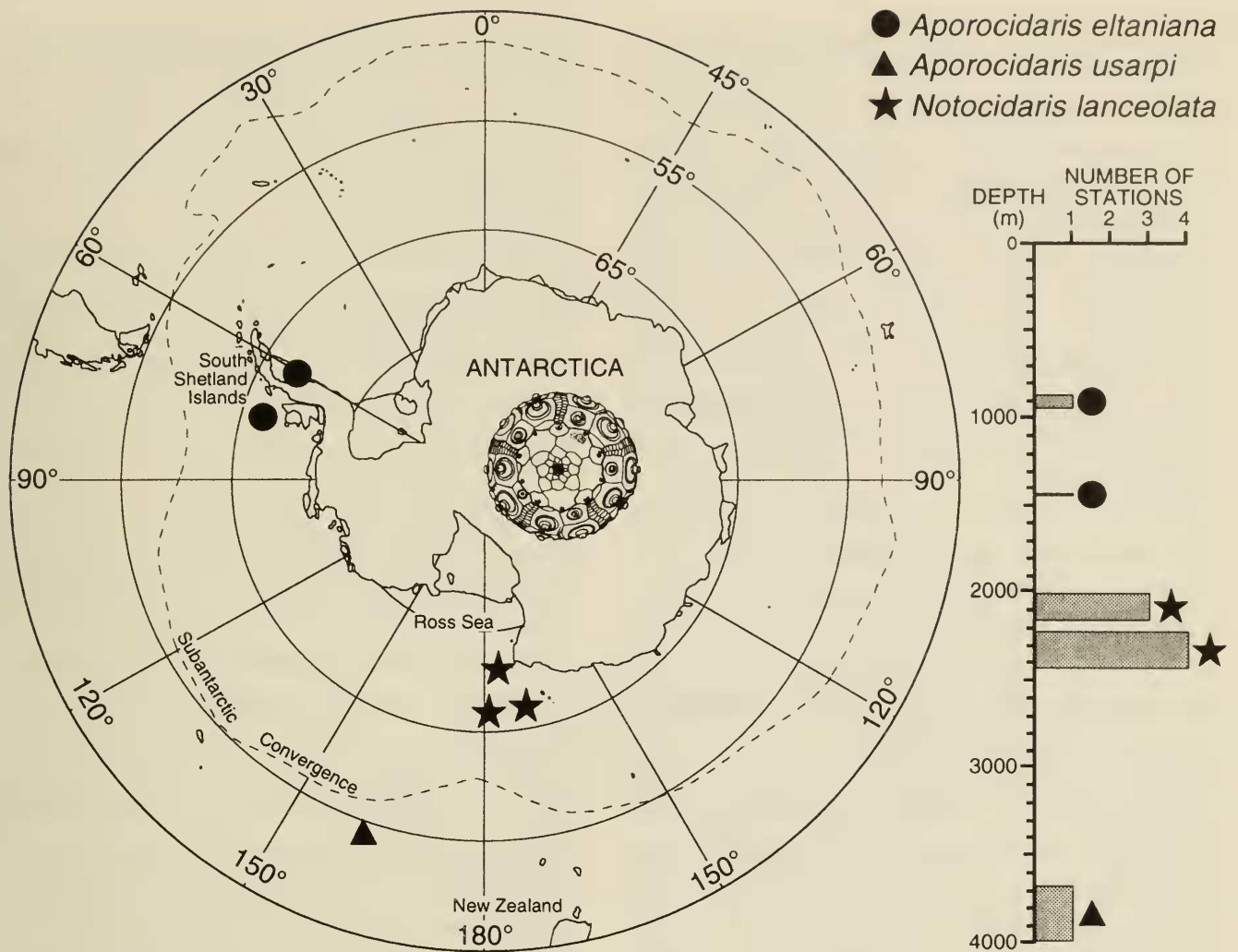


Fig. 1. Collecting localities and recorded depths (graph at right) for *Aporocidaris eltaniana* new species, *A. usarpi* new species, and *Notocidaris lanceolata* new species. Number of stations refers to the number of R/V *Eltanin* stations that for a given species fall within the depth range indicated by the height of the shaded box.

so until a more complete knowledge of the taxonomy is established. The lack of consistent, well-delineated features as well as detailed analyses of morphological variation makes the Antarctic cidaroids a particularly difficult group, as evidenced by the almost unusable keys provided by previous major revisions such as Mortensen (1928). In addition, material is often rare, and several taxa are represented only by juveniles, or have not been collected since they were first described from single or very few individuals. Therefore, determination of terminal taxa to be used in phylogenetic analysis is in its infancy, and any effort to place the taxa described here in an evolutionary context is premature.

Jackson (1912) and Smith (1984) provided excellent comparative overviews of ci-

daroid morphology. Cidaroids are very easy to separate from other types of regular urchins. Each interambulacral plate bears a single, large, perforate primary tubercle supporting a primary spine that is strongly differentiated from the secondary spines covering the rest of the test. Primaries are many times larger than secondaries, and much more robust. The shafts of adult cidaroid primary spines are unique not only among all spines on a cidaroid, but also among echinoids in general in completely lacking an epithelial layer. These spines are often invested with various epizoans such as sponges, serpulids, bryozoans, and small mollusks. Each primary is encircled by a palisade of much shorter secondary spines called scrobiculars that can be appressed to the base of the primary spine.



In contrast to other regular echinoids, cidaroid ambulacra are very narrow relative to the interambulacra. The ambulacral plates are arranged in two simple columns, each of which bears a single tube foot pore (usually bipartite), and one to several small secondary spines. The ambulacral series continue to the mouth on the peristomial membrane, and the number of peristomial ambulacrals can be helpful in discriminating certain Antarctic taxa. The perignathic girdle consists of interambulacral processes called apophyses. The Aristotle's lantern of Antarctic species is typical for cidaroids, and does not vary enough to form the source of characters that could be used to distinguish the taxa.

Although it is relatively easy to recognize a cidaroid, a confounding feature of the taxonomy within the group is conservatism in plate architecture and overall form of the test. However, the cidaroids more than compensate for this conservatism in diversity of primary spine morphology. The taxa described in this paper exemplify the fact that many cidaroid species cannot be identified without information on the primary spines. Both scrobicular and non-scrobicular secondary spines can also be useful in diagnosing Antarctic cidaroids.

Cidaroids are epibenthic and inhabit various environments from sandy and stony bottoms in littoral zones to gravels and muds of sub-littoral regions. They are also common in the deep-sea on muddy bottoms of bathyal slopes or abyssal plains to 5000 meters, and they constitute a significant part of the benthic community at these depths. Many, if not all, of the Antarctic cidaroids are direct developers, as suggested by the fact that in almost every species, a subset of adults presumed to be females have greatly enlarged gonopores. Fell (1976) and Lockhart et al. (1994) recorded that many species also brood their young in and around "marsupia" created by the more or less sunken peristome, a feature of which we make special note in the following descriptions. Because the presence of brooded

young is correlated with enlarged gonopores, and because large gonopores are known to signify females in other echinoids, we also use the presence of enlarged gonopores and marsupia to infer gender in adult specimens.

Upon occasion, primary spines of Antarctic cidaroids also support a very poorly understood parasite, *Echinophyces mirabilis* Mortensen & Rosenvinge, 1909. The occurrence of this parasite is correlated with some modifications of the infected echinoid's morphology and a delay in the appearance and change in position of the gonopores. The mechanism by which a parasite of a more or less biologically inert external feature such as the cidaroid spine can affect the expression of gonads and gonopores is totally unknown and clearly deserves further study. It is surprising that virtually no research beyond the original description and that of Mortensen & Rosenvinge (1910) has been done on this unusual phenomenon. Fell (1976), Jangoux (1987), and Pearse & Cameron (1991) have summarized what few data exist, finding that *Echinophyces* is found only in *Ctenocidaris* Mortensen, 1910 and *Rhynchocidaris* Mortensen, 1909. We report on the results of our as yet unsuccessful search for evidence of this parasite in the new species, in the hope that future studies might be able to use even these negative data.

Order Cidaroida L. Agassiz, 1835

Family Cidaridae Gray, 1825

Genus *Aporocidaris* A. Agassiz & Clark,  
1907

*Diagnosis.*—Ctenocidarine cidarids with a large apical system which can be as much as 75% of the horizontal diameter of the test. Apical system often significantly domed or convex. Mid-interambulacral regions usually with a slightly depressed, naked interradiial suture.

*Remarks.*—Mortensen (1928) considered four nominal species in the genus *Aporocidaris*, but he emphasized the "exceeding-

ly slight" differences between 3 of them: *A. antarctica* Mortensen, 1909, *A. fragilis* A. Agassiz & Clark, 1907, and *A. milleri* (A. Agassiz, 1898). Fell (1976) proposed synonymy of these 3 species under *A. milleri* but suggested a new species, *A. eltaniana*. In an unpublished manuscript, Cheshier recognized yet another species, *A. usarpi*. We introduce the latter names to the published literature for the first time.

*Aporocidaris eltaniana*, new species

Fig. 2

*Aporocidaris eltaniana*.—ex Fell, 1976: 211, figs. 7, 8j–k, name used in unpublished thesis.

*Diagnosis*.—Apical system as much as 68% of test diameter. Aboral primary tubercles large and markedly transversely oval at ambitus. Aboral primary spines cylindrical, 1 to 1.5 times test diameter, mostly smooth or with small bumps arranged in longitudinal rows; tip blunt, or slightly concave. Oral primary spines with conspicuous thorns along lateral edges of shaft. Preserved specimens dark brown, primary spines whitish, secondary spines beige to light brown. Other characters as for *Aporocidaris*.

*Description*.—The test is about half the height of the horizontal diameter, but the height of the apical system is quite variable and can add as much as 20% to the overall height of the coronal part of the test. The largest recorded size of the specimens examined is about 45 mm in horizontal diameter of the test. The holotype is 29.3 mm in diameter, 16.9 mm high, has an apical system diameter of 15.6 mm and a peristome diameter of 12.5 mm.

The ambulacra are almost straight (Fig. 2A, B), particularly on the oral surface, and their tuberculation is of the usual *Aporocidaris* pattern (Fig. 2E). There is no naked area along the perradial suture. The inner and outer pore of each podial pore pair are divided by a well-developed "bridge" of stereom (Fig. 2E).

The interambulacra have about one more plate in each series than *A. milleri* of similar size. The crowding of the plates into the relatively flat corona, and the size of the tubercles between the ambitus and the peristome cause the tubercles to be compressed into horizontally oriented ovals (Fig. 2B). The scrobicular tubercles are more than twice the diameter of the other secondary tubercles, and surround each primary tubercle except where the oval outlines of the primaries touch (Fig. 2D). The interradian suture is conspicuously sunken in larger specimens (Fig. 2D).

The apical system is large (about 60% of the horizontal diameter on average), and almost flat or only slightly domed in most specimens. However, a few exceptional individuals have a strongly arched apical region that can account for over a fifth of the total height of the test. The genital plates are large, with scattered secondary tubercles. In males, the gonopores are small and close to the outer edges of the genital plates (Fig. 2A). In several of the specimens, the gonopores are large, forming notches that in extreme cases can extend part way along the interradian suture separating the interambulacral plates adjacent to the genital. Like Fell (1976), we have assumed these specimens to be females. The gonopores first appear in specimens as small as 16 mm in test diameter. Ocular plates are only about a third the area of the genitals, and the ocular pores are surrounded by a circular ridge that seems to be most pronounced in the males (Fig. 2A). Tuberculation is not dense, and restricted to the central parts of the plates over the majority of the apex (Fig. 2A).

The peristome is just over 55% of the test diameter in small specimens, but becomes smaller in larger individuals (approximately 40% of the test diameter), relative to test diameter. The peristome itself is somewhat sunken around its periphery, notably in the interambulacral regions. Seven to 8 pairs of ambulacral plates continue onto the peristome in larger specimens, and there are



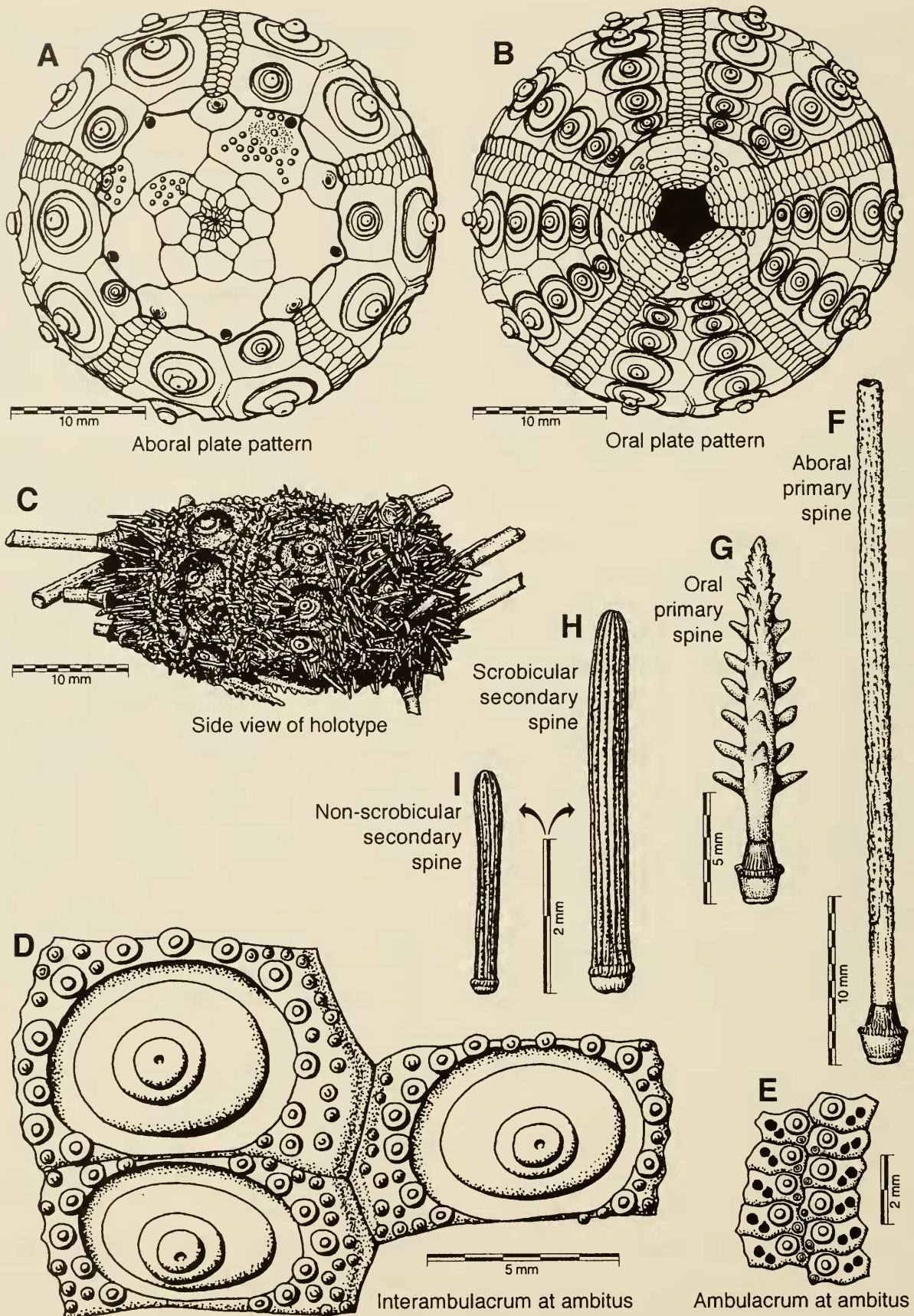


Fig. 2. *Aporocidaris eltaniana* new species. C drawn from holotype (NMNH E48122); A, B, D-I drawn from paratypes in lot NMNH E11161. For A and B: mouth, anus, and gonopores in solid black; podial pores omitted; secondary tubercles shown only for single genital, ocular, and periproctal plates, but omitted elsewhere, including coronal plates.

only 2 or 3 small scales in each interradial region (Fig. 2B).

The longest aboral primary spines found (on the almost intact specimens in NMNH E11161) are approximately 1.5 times the test diameter and rod-like with blunt or slightly concave tips and large milled rings (Fig. 2F). The surface of the shaft is smooth proximally, but bears small, longitudinally aligned, blunt spinules for more than 80% of its length out to the tip (Fig. 2F). The flat areas between the longitudinal rows are covered with a variously developed fibrous and anastomosing calcareous meshwork. The oral primaries are strongly curved towards the peristome, and bear well developed thorns that project laterally, but become smaller towards the tip of the spine. There is often another row of shorter thorns along the distal part of the shaft (Fig. 2G). The more or less cylindrical scrobicular spines are blunt, but not club-shaped (Fig. 2H). The non-scrobicular secondaries are much shorter than the scrobicular spines and sometimes slightly curved near the almost imperceptibly swollen tip (Fig. 2I).

The small globiferous pedicellariae are rare, but appear simply to be half-sized versions of the larger type. The stem of a globiferous pedicellaria is thick, and straight. Neither the valves nor stem are otherwise distinctive among *Aporocidaris* species (Mortensen 1928).

*Types*.—Holotype NMNH E48122, extracted from NMNH E11161, R/V *Eltanin* Cruise 6, Station 432 (Fig. 2C). Paratypes NMNH E11161 (3 dry specimens, one dissected lantern), E11188 (17 dry specimens, including 3 less than 10 mm in horizontal test diameter), E11212 (dry spines only), E11290 (more than 60 dry specimens), E14597 (2 specimens greater than 28 mm in test diameter, the largest of which is a female with more than 12 young urchins brooded on the peristome, 1 specimen 14.3 mm in horizontal test diameter, and 16 specimens less than 10 mm in test diameter, all in alcohol), MCZ 8406 (1 dry specimen). The holotype was chosen because it

retained significant spine cover (Fig. 2C). The paratypes in NMNH E11161 were used to make the drawings of plate architecture so as not to disturb what spination remains on the holotype.

*Etymology*.—Named for U.S. National Science Foundation R/V *Eltanin*. The species name was first coined in an unpublished doctoral thesis by Fell (1976), and we introduce the name here in recognition of that first usage.

*Distribution*.—*A. eltaniana* is known only from the type series, which was collected from two R/V *Eltanin* stations (Cruise 4, Station 138; Cruise 6, Station 432) at two distinct localities, both in the region of Livingston Island in the South Shetland Islands, between 884 and 1437 m depth (Fig. 1).

*Biology*.—The gonopores in females may reach 1.8 mm in diameter. One female (NMNH E14597), 43.4 mm in horizontal test diameter, had more than a dozen juvenile urchins in the marsupium along the sunken edge of the peristomial margin. An exact count of the juveniles was impossible without damaging the adult specimen. Most of the young were obscured by oral primary and secondary spines that folded over to screen the deepest parts of the marsupium in the interambulacral areas proximal to the edge of the coronal plates. One of the largest of the juveniles was 2.2 mm in horizontal test diameter, and all of the brooded young possessed primary spines, the longest of which were approximately 2.0 mm long. These observations suggest that juveniles of *A. eltaniana* develop directly from relatively large eggs which are moved into, and then develop in a peristomial marsupium. None of the specimens appear to be infected by *Echinophyces*. Nothing is known of the preferred bottom type, but the gut contents of one specimen are made up of light gray silt containing small fragments of thin mollusk shells.

*Remarks*.—The greatly enlarged apical system and the naked, sunken area along the interradius indicate that the new species



is an *Aporocidaris*. *A. eltaniana* is most similar to *A. milleri*, but is distinct from all *Aporocidaris* in possessing strongly developed thorns on the oral primary spines. The dramatic difference between the relatively smooth, cylindrical aboral primaries and the thorny oral primaries is unmatched in the genus, if not within the Antarctic cidaroids in general.

*Aporocidaris usarpi*, new species

Fig. 3

*Diagnosis.*—Apical system as much as 70% of test diameter in adults. Aboral primary spines cylindrical, 1 to 1.5 times test diameter, with small, irregularly distributed or only slightly aligned bumps distally. Neck of aboral primaries glossy, porcellaneous, and markedly swollen in larger specimens. Oral primary spines flattened with lateral, diametrically opposed, serrated keels that are widest just distal to neck and taper towards spine tip. Scrobicular spines fine, small, closely spaced, and not strongly differentiated from the non-scrobicular spines. Both types of secondary spines slightly club-shaped. Preserved specimens beige, primary spines white, secondary spines light beige. Other characters as for *Aporocidaris*.

*Description.*—The test is only moderately flattened. The height of small specimens is just over 50% of the horizontal diameter, but in larger specimens, the height is greater (up to 75% of the horizontal diameter), almost 15% of which can be in the form of the domed apical system (Fig. 3C). The largest specimen is just over 40 mm in horizontal diameter. The holotype is 35.2 mm in diameter, 23.4 mm high, has an apical system diameter of 23.0 mm and a peristome diameter of 15.2 mm.

The ambulacra are almost straight (Fig. 3A, B), particularly on the oral surface, and their tuberculation is of the usual *Aporocidaris* pattern, with smaller secondary tubercles adjacent to the perradial suture, and slightly larger ones just distal to those (Fig.

3E). There is no naked region along the periradius. In the holotype and the largest of the paratypes (NMNH E11059), the “bridge” between the pore pairs on each ambulacral plate is incomplete so that the pores are connected via a constricted passage between the pores (Fig. 3E). This condition is rare, if not unique among Antarctic cidaroids.

The interambulacral plates are high. Aborally, the primary tubercles do not occupy the entire height of the plate so that the aboral primary tubercles retain their round outlines. However, adjacent to the peristome, the tubercles are more crowded, and tend to compress slightly into transverse ovals (Fig. 3B). The scrobicular tubercles are not strongly differentiated in size from the non-scrobicular secondaries, which are small and closely spaced everywhere outside the primary tubercle except along the interradius, where tubercles are lacking (Fig. 3D). This distinct naked area is adjacent to each interradial suture and occupied by a shallow furrow that, in larger specimens, sends branches circumferentially along sutures separating plates in each of the two interambulacral columns (Fig. 3D).

The apical system is large, ranging from just over 50% of the test diameter in juveniles to over 70% of the diameter in the largest adults. In the juveniles, the apical region tends to be almost flat. It is distinctly domed in adults, with considerable irregular inflation of the centers of some of the larger apical plates (particularly the genitals), especially in the specimen identified as a female. The genital plates are large relative to the other plates in the apical system. In the largest paratype, which appears to be a female, the gonopores can be as much as 2.4 mm in diameter and in some cases occupy shallow clefts along the interradial suture (Fig. 3A). The gonopores are present in the holotype, which appears to be a male, but are not evident in the larger of the 2 small paratypes in NMNH E11059, which is 13.9 mm in diameter. Ocular plates are only about a quarter the area of the genitals, and the ocular pores are surrounded by a

prominent circular ridge (Fig. 3A). The tuberculation on both oculars and genitals is fine and dense, and tends to cover the entire plate surface almost to the suture (Fig. 3A).

The peristome is sunken around its periphery, and in the region of half the test diameter. Each perradial region bears 8 or 9 plates in each ambulacral column, and there are two relatively large scales in each interradian portion of the membrane (Fig. 3B).

The longest aboral primary spines are approximately 1 to 1.5 times the horizontal diameter of the test, although even the best examples are worn or broken so that the nature of the tips cannot be ascertained. Distal to the neck, the shaft is cylindrical and rod-like, and invested with irregularly spaced to only partially aligned, short, blunt spinules or bumps that arise from the smooth, porcellaneous surface. The neck is most peculiar in that it is greatly swollen in primary spines of larger specimens, and completely unadorned with spinules. The surface of the swelling is smooth, porcellaneous and glossy, and increases the diameter of the spine by a factor of 2 at its widest point (Fig. 3F). In juvenile specimens, the neck is also porcellaneous but only slightly swollen, suggesting that the vase-like shape of the swelling becomes more prominent with age. The oral primary spines are only slightly curved towards the peristome, and bear diametrically opposing flanges or keels along the lateral sides of the shaft. The edges of these keels are finely serrated, and the keels themselves are widest proximally, tapering towards the relatively blunt spine tip to give the entire spine a dagger-like appearance (Fig. 3G). The surface of the oral primaries is smooth and shiny, but not as glossy as the aboral primaries. The almost cylindrical scrobicular spines are blunt and very slightly swollen towards the tip (Fig. 3H). Scrobicular secondaries are only slightly longer than the non-scrobicular secondary spines (Fig. 3I). Both types of secondaries are club-shaped.

The valves of the large globiferous ped-

icellariae are less than 1 mm in length, and very similar to those of other *Aporocidaris* (Mortensen 1928). The smaller globiferous were not detected.

*Types*.—Holotype NMNH E11134, R/V *Eltanin* Cruise 14, Station 1212 (Fig. 3C, F–I). Paratypes NMNH E11059 (3 dry specimens, one dissected lantern, and one almost perfect, loose spine), E14603 (1 specimen in alcohol). The holotype was chosen because it retained some spines (Fig. 3C). Plate architecture was drawn from one of the largest of the paratypes in NMNH E11059 to avoid further damage to the holotype.

*Etymology*.—The name "*A. usarpi*" was originally used by Dr. Richard Chesher in his identifications of USARP material now housed the NMNH (see above), and it is clear from notes placed with that material that he intended to publish the species in a manuscript that never saw press. We retain Chesher's suggested name in honor of his recognition of the distinctiveness of this taxon.

*Distribution*.—*A. usarpi* is known only from a single R/V *Eltanin* locality (Cruise 14, station 1212) from a mid-ocean point far to the southeast of New Zealand and north of the Ross Sea (Fig. 1) at a depth of between 3678 and 3935 m.

*Biology*.—Nothing is known of the habitat preferences of *A. usarpi*, and appropriate specimens could not be sacrificed for gut content observations. There is some sexual dimorphism. The putative female has greatly enlarged gonopores (up to 2.4 mm in diameter) relative to the putative male, suggesting direct development in this species. None of the specimens had young retained on the test, although the peristomial edge is slightly sunken in such a way as to suggest the same type of marsupia seen in other species bearing young on the peristome. None of the specimens show obvious signs of *Echinophyces* infection, but the paucity and condition of the material prevent us from ruling out the occurrence of the parasite in *A. usarpi*.



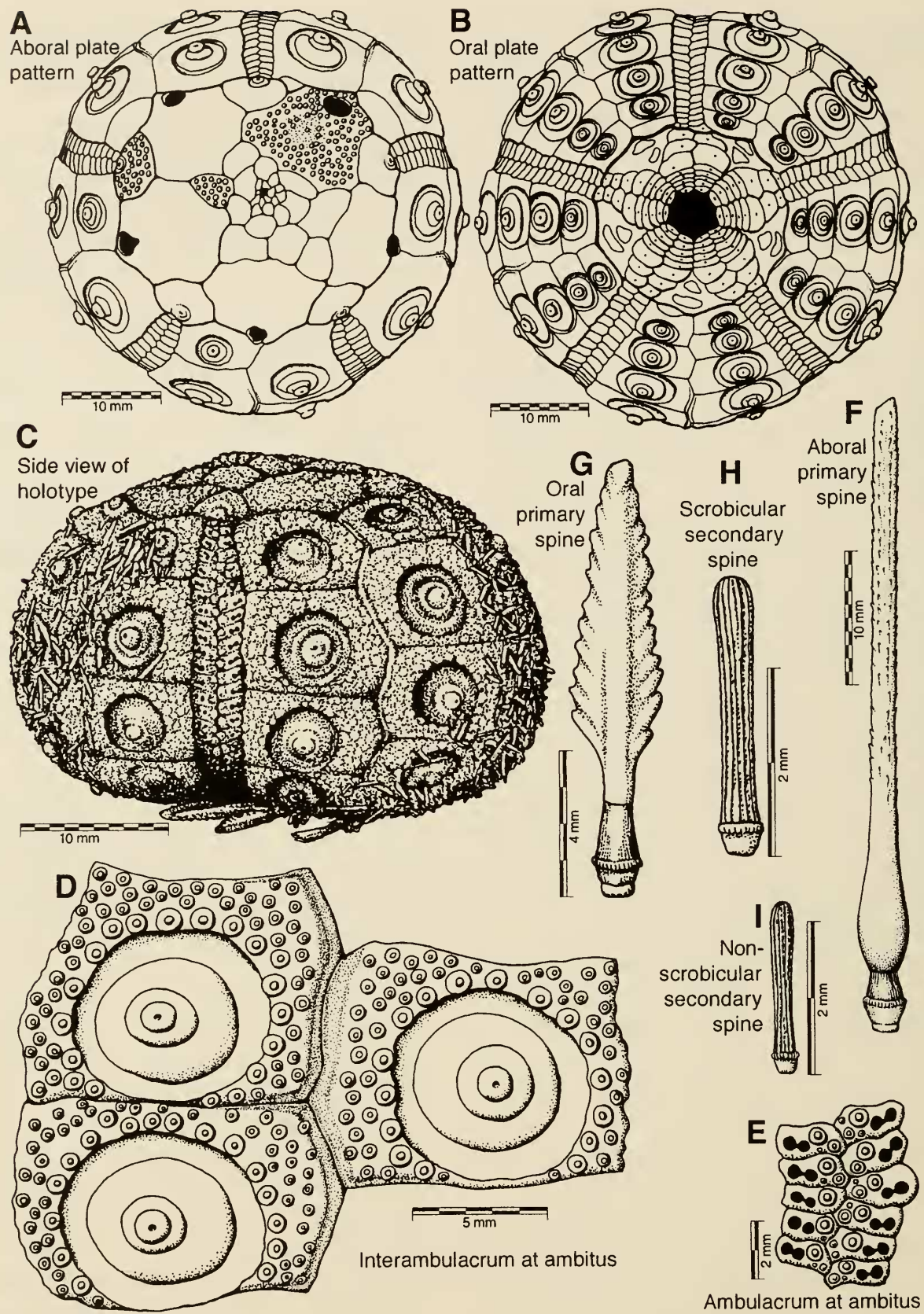


Fig. 3. *Aporocidaris usarpi* new species. C, F-I drawn from holotype (NMNH E11134); A, B, D, E drawn from paratypes in lot NMNH E11059. Conventions for A and B as in Fig. 2.

*Remarks.*—The greatly enlarged apical system and the naked, sunken area along the interradius indicate that the new species is an *Aporocidaris*. The species is readily distinguished from all other *Aporocidaris* by the peculiar swelling of the neck in the primary spines, and the extreme glossiness of both this swelling, and the shaft of the spines between the distal spinules. The absence of stereom bridges separating the members of the podial pore pairs has not been previously reported for any ctenocidarine taxa, let alone other *Aporocidaris*. Both the holotype and the largest of the paratypes exhibit this feature, but the two smallest specimens (below 14 mm horizontal diameter) have clearly divided pores, suggesting that the unification of the pores progresses with ontogeny, and is a derived feature of adult *A. usarpi*.

#### Genus *Notocidaris* Mortensen, 1909

*Diagnosis.*—Oral primary spines spear- or dagger-shaped. Aboral primaries rod-like and cylindrical to flattened and spatulate, with large lateral expansions distally. Spines smooth or spiny, but when present, spinules restricted to proximal part of shaft. Proximal surface of spines occasionally with coating of anastomosing hairs. Scrobicular secondary spines simple and slender (but not as fine or densely distributed as in *Aporocidaris*), not distinct in shape from other secondary spines. Interradial sutures naked, but not sunken. Apical system about 60% of horizontal diameter.

*Remarks.*—Mortensen (1928) listed 4 species in the genus: *N. gaussensis* Mortensen, 1909, *N. hastata* Mortensen, 1909, *N. mortenseni* (Koehler, 1900), and *N. platyacantha* (H. L. Clark, 1925). Another species, *N. remigera* Mortensen, 1950 was described after Mortensen's monograph of the cidaroids was published. We do not consider the entity *N. platyacantha* var. *contracta* Koehler, 1926 to be a valid taxon. Therefore, we attribute 5 full species to *Notocidaris*, all from Antarctic and Subantarctic

waters, and all distinguished by features of the aboral primary spines. It should be noted that the range of variation recorded for each species can be extremely large and spine characteristics can overlap for species such as *N. remigera* and *N. mortenseni*. Therefore, biogeographic and bathymetric data, as well as other parts of the descriptions must also be used to make positive determinations.

#### *Notocidaris lanceolata*, new species

Fig. 4

*Notocidaris lanceolata.*—ex Fell, 1976: 195; figs. 7, 8f-g, name used in unpublished thesis

*Diagnosis.*—Aboral primary spines coarsely thorned at their base, with thorns arranged irregularly, and becoming greatly reduced in size and aligned towards tip. Spines keeled in two orthogonal planes in cross section, yielding lance-like appearance, spine tapering slightly towards relatively blunt tip. Longest spines about 2 times horizontal diameter of test in most specimens. Apical system varying from flat to arched. Test of preserved specimens beige to ochre, primary spines beige with shiny purplish-beige neck, secondary spines beige. Other characters as for *Notocidaris*.

*Description.*—The largest recorded horizontal test diameter is 36 mm. The height is between 50% and 60% of the test diameter. The holotype is 32.5 mm in horizontal diameter and 19.4 mm high.

The ambulacra are straight on the oral surface, with some slight sinuousness aborally (Fig. 4A, B). There are one or two secondary tubercles perradial to the podial pores, and two or three much smaller secondary tubercles next to the perradial suture (Fig. 4E). There is no naked region along the perradius. The inner and outer pore of each podial pore pair are divided by a well-developed "bridge" of stereom (Fig. 4E).

The aboral interambulacral plates are high and the primary tubercles are circular. Orally, the plates are not as high and the



tubercles are compressed into transverse ovals (Fig. 4B). There are 7 or 8 plates in each column in a specimen about 50 mm in diameter. The scrobicular tubercles are in general only slightly differentiated from the non-scrobicular secondaries, which are abundant and closely spaced except along the interradiial suture, where tubercles are lacking (Fig. 4D). There is no sunken area along the interradiial suture.

The apical system is usually about 60% of the test diameter in larger specimens, and can range from being flat, as in the holotype, to domed. The gonopores are restricted to the genital plates and do not significantly invade the adjoining interambulacra. The females have enlarged gonopores. The oculars are large and circumferentially elongated so that they are much wider than they are high, and about half the surface area of the genital plates (Fig. 4A). The ocular pore is encircled by a prominent ridge and the tuberculation is fine and evenly distributed across each plate in the apical system except directly adjacent to the sutures (Fig. 4A).

The peristome is only slightly sunken at its periphery, and approximately 45% of the test diameter. There are 7 or 8 plates in each ambulacral column on the peristome of larger specimens, and as many as 5 small, irregularly shaped scales in each interradiial portion of the membrane (Fig. 4B).

The ambital and aboral primary spines can be up to 2 times the diameter of the test and tapered. Several complete examples remain attached to the holotype (Fig. 4C). Near the base, the spine is adorned with irregularly arranged, prominent thorns and serrations which diminish sharply in size about 30% of the spine's length away from the base, giving way to strongly aligned, distal rows of spinules (Fig. 4F). Although the cross-section of the spine is broadly circular, usually there are also well-developed keels set almost orthogonally to each other along the distal part of the spine. The degree to which these keels are developed varies among specimens and even on an in-

dividual, but the basal thorns seem to be a constant feature. Basally, the spine can bear a surface coat of anastomosing hairs similar to that seen in some *Aporocidaris*. The oral primaries differ from the aboral primaries in lacking strongly developed keels except laterally, where they can also be strongly serrated (Fig. 4G), particularly in specimens with thorny aboral primaries. The oral primaries adjacent to the peristome are very small and dagger- or arrowhead-shaped, with somewhat less distinctly serrated keels. In specimens with reduced keels on the aboral primaries, the oral primaries are less dagger-shaped, and more oval in outline. The scrobicular spines are slightly pointed (Fig. 4H). The non-scrobicular secondary spines are smaller, particularly in the ambulacra (Fig. 4I).

As in most ctenocidarines, the globiferous pedicellariae come in two sizes, both of which are quite long and slender in *N. lanceolata*, though not diagnostically so. The valves can be just over 1 mm long in the larger form.

*Types*.—Holotype MCZ 8336, R/V *Eltanin* Cruise 32, Station 2110 (Fig. 4C). Paratypes NMNH E21865 (3 dry specimens), E21866 (1 dry specimen), E22004 (1 specimen in alcohol), E22005 (5 specimens in alcohol), E22006 (3 specimens in alcohol). We decided to retain the holotype designated in Fell (1976) to avoid confusion, and also because the specimen has exemplary spine cover (Fig. 4C). Drawings of spines and plate architecture were made from the paratypes to avoid damaging the holotype.

*Etymology*.—In his thesis, Fell (1976) attributed the name to Richard Cheshier, who recognized the distinctiveness of the new taxon in a manuscript that was never published. Cheshier based the name on the keeled, lanceolate spines.

*Distribution*.—Known from 7 R/V *Eltanin* stations (Cruise 27, Stations 1867, 1926, 1929; Cruise 32, Stations 2002, 2108, 2110, 2129) at three distinct localities in the

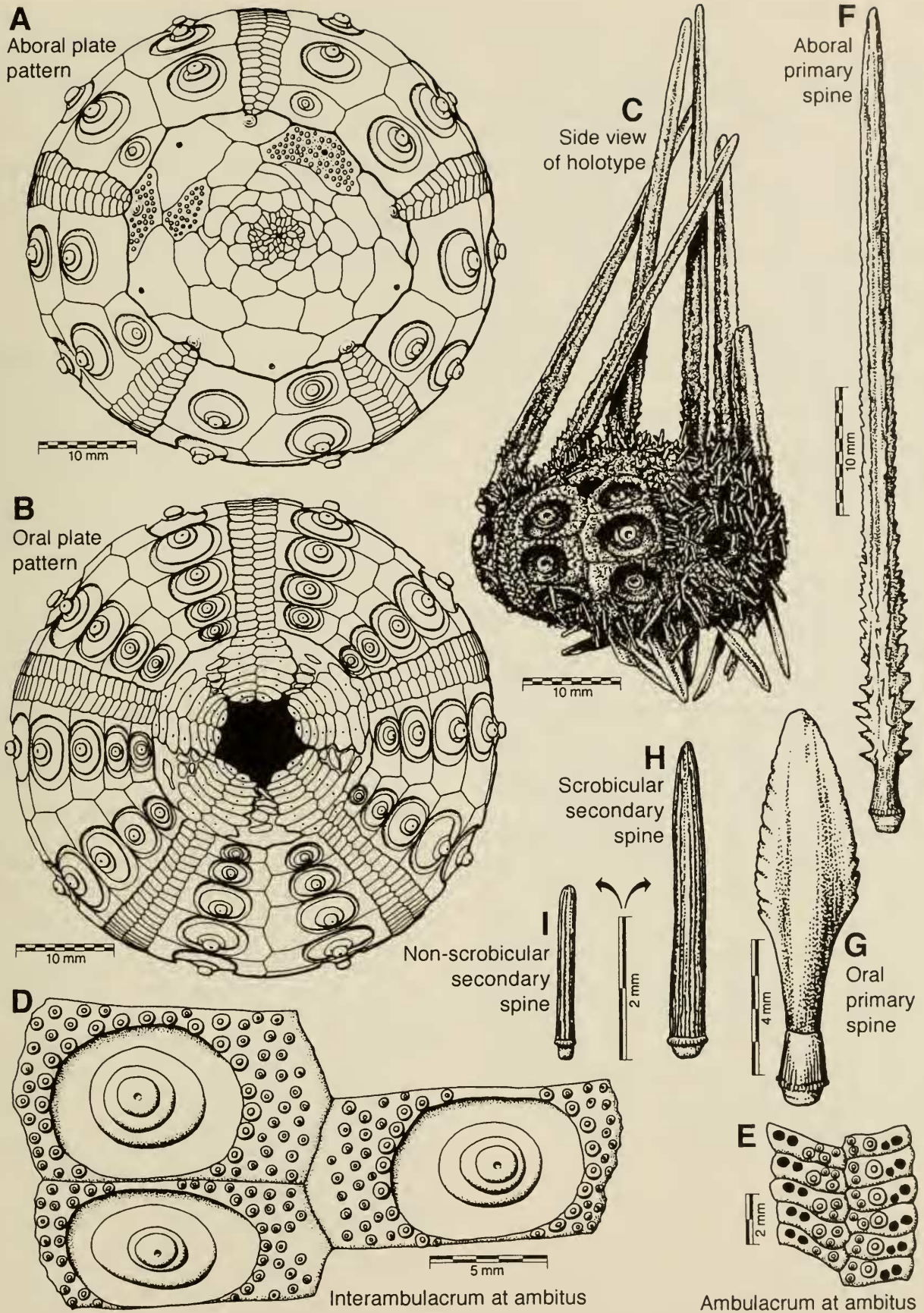


Fig. 4. *Notocidaris lanceolata* new species. C drawn from holotype (MCZ 8336); A, B, D, E drawn from paratypes in lot NMNH E21865; F-I drawn from paratype (NMHH E 21866). Conventions for A and B as in Fig. 2.



Ross Sea between 2005 and 2421 m (Fig. 1).

**Biology.**—The spines seem remarkably free of epizoans. The preferred habitat is unknown. Some specimens, which could be females, have enlarged gonopores, but no broods have been observed. No evidence of *Echinophyces* infection could be detected.

**Remarks.**—As noted by Fell (1976:197), the species was based on a specimen rescued by Dr. Merrill Foster from “material intended for disposal overboard” and later turned over to Chesher, who selected it as a potential type. The holotype, in having primaries that are thorny and strongly lanceolate, is close to one end of a range that includes forms in which the keels can be almost absent. As Fell (1976:197) indicated, “were it not for the range of intermediates between fluteless [unkeeled] and fully fluted [keeled] specimens obtained at two stations, one would not believe they were of a single species”. Typical *N. lanceolata* may be most easily confused with particularly thorny *N. hastata*, especially since they inhabit the same environments, while variants of *N. lanceolata* with greatly reduced keels on the spines may be confused with *N. gaussensis*. In addition, the surface coating of anastomosing hairs between the thorns and keels near the base of the spine can cause some confusion with *Ctenocidaris*, particularly if this feature alone is used to sort material. Because *N. lanceolata* occurs, on average, almost 1000 m deeper than *N. gaussensis* and virtually all *Ctenocidaris*, available depth data should help to provide initial clues in identification.

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#### Literature Cited

- Agassiz, A. 1898. Reports on the dredging operations off the west coast of Central America to the Galápagos, to the west coast of México, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer “Albatross,” during 1891, Lieut. Commander Z. L. Tanner, U.S.N., Commanding. XXIII. Preliminary report on the Echini.—Bulletin of the Museum of Comparative Zoology 32:71–86.
- , & H. L. Clark. 1907. Hawaiian and other Pacific Echini. Cidaridae.—Memoirs of the Museum of Comparative Zoology at Harvard College 34(1):1–42.
- Agassiz, L. 1835. Prodrôme d'une monographie des radiaires ou échinodermes.—Mémoires de la Société des Sciences Naturelles de Neuchâtel 1: 168–199.
- Clark, H. L. 1925. A Catalogue of the Recent Sea-Urchins (Echinoidea) in the Collection of the British Museum (Natural History). Trustees of the British Museum, London, England, 250 pp.
- David, B., & R. Mooi. 1990. An echinoid that “gives birth”: morphology and systematics of a new Antarctic species, *Urechinus mortenseni* (Echinodermata, Holasteroidea).—Zoomorphology 110:75–89.
- Fell, F. J. 1976. The Cidaroida (Echinodermata: Echinoidea) of Antarctica and the southern oceans. Unpublished Ph.D. Dissertation, University of Maine, Orono, 294 pp.
- Gray, J. E. 1825. An attempt to divide the Echinida, or sea eggs, into natural families.—Annals of Philosophy, new series 10:423–431.
- Jackson, R. T. 1912. Phylogeny of the Echini, with a revision of the Paleozoic species.—Memoirs of the Boston Society of Natural History 7:1–490.
- Jangoux, M. 1987. Diseases of Echinodermata. I. Agents microorganisms and protists.—Diseases of Aquatic Organisms 2:147–162.
- Koehler, R. 1900. Note préliminaire sur les échinides et les ophiures de l'expédition antarctique belge.—Bulletin de l'Académie Royale Belge, Series 3, Sciences 38:814–820.
- . 1926. Echinodermata Echinoidea. Pp. 1–134

- in* L. Harrison, ed., Scientific Reports, Series C, Zoology and Botany, Australasian Antarctic Expedition, 1911–1914, Under the Leadership of Sir Douglas Mawson, D.Sc., B.E., F.R.S., vol. 8(3). Alfred J. Kent, Government Printer, Sydney, Australia, 134 pp.
- Lockhart, S. J., P. M. O'Loughlin, & P. Tutera. 1994. Brood-protection and diversity in echinoids from Prydz Bay, Antarctica. Pp. 87–95 *in* B. David, A. Guille, J.-P. Féral, & M. Roux, eds., Echinoderms through time (Echinoderms Dijon). A. A. Balkema, Rotterdam, Netherlands, 940 pp.
- Mortensen, T. 1909. Die Echinoiden der Deutschen Südpolar-Expedition 1901–1903.—*Deutsche Südpolar Expedition* 11:1–113.
- . 1910. The Echinoidea of the Swedish South Polar Expedition.—*Schwedische Südpolar-Expedition 1901–1903*, 6:1–114.
- . 1928. A monograph of the Echinoidea, 1. *Cidaroida*. C. A. Reitzel, Copenhagen, Denmark, 551 pp.
- . 1950. British Australian New Zealand Antarctic Research Expedition, 1929–1931, Echinoidea.—*BANZAR Expedition Reports, Series B (Zoology and Botany)* 4:287–310.
- , & L. K. Rosenvinge. 1910. Sur quelques plantes parasites dans des échinodermes.—*Académie Royale des Sciences et des Lettres de Danemark* 1910(4):339–354.
- Pearse, J. S., & R. A. Cameron. 1991. Echinoidea. Pp. 513–662 *in* A. C. Giese, J. S. Pearse, & V. B. Pearse, eds., Reproduction of marine invertebrates, vol. VI. Echinoderms and Lophophorates. Boxwood Press, California, 808 pp.
- Smith, A. B. 1984. Echinoid palaeobiology. Allen and Unwin, London, England, 190 pp.
- , & C. W. Wright. 1988. British Cretaceous echinoids. Part 1, General introduction and *Cidaroida*. Monograph of the Palaeontographical Society, London—141:1–101.